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REMAINS OF *ARTHROPLEURA*, A GIGANTIC MYRIAPOD ARTHROPOD, FROM THE PENNSYLVANIAN OF OHIO AND PENNSYLVANIA

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ABSTRACT

Fossils attributed to *Arthropleura* Jordan, a genus of gigantic myriapod arthropod, are described from lower Conemaugh (?Missourian) rocks at the 7-11 site, a strip mine in Columbiana County, Ohio, and from Allegheny (Desmoinesian) rocks at Cannelton, Beaver County, Pennsylvania. The specimens from these localities consist primarily of rosette and B plates, body parts that would have been closely associated with limbs of the organism in life. The Ohio specimen represents an animal whose length exceeded 1.5 m; the Pennsylvania specimen probably represents a smaller, but still large, individual. The Ohio arthropleurid is probably conspecific with *Arthropleura cristata* Richardson, which belongs to the Desmoinesian Mazon Creek, Illinois, fauna. The specimen from Pennsylvania may also belong to the same species.

Introduction

Arthropleurids are a group of myriapod animals that includes the largest known terrestrial arthropods. Fossils of arthropleurids are known from Upper Silurian (Přídolí) through at least Upper Carboniferous (Stephanian) rocks (Shear and Kukalová-Peck, 1990; Ross and Briggs, 1993; Briggs and Almond, 1994; Shear and Selden, 1995). The largest and most common genus of arthropleurid is *Arthropleura* Jordan, which is usually cited as being restricted to the Carboniferous. Barthel and Schneider *(in* Barthel and Rössler, 1995, p. 7), however, have recently noted an occurrence in the Lower Rotliegend which may extend the range of *Arthropleura* into the Lower Permian. About 10 species of *Arthropleura* have been described from Europe (Almond, 1985) and two have been described from North America. Many of the species of *Arthropleura* were of gigantic size.

Body fossils referable to the genus *Arthropleura* have been described from a number of countries in western and central Europe, including Britain, France (Briggs and Almond, 1994), the Netherlands and Germany (Hahn et al., 1986), and the Czech Republic (Spinar, 1960), as well as Kazakhstan (Novozhilov, 1962). These occurrences range from the Westphalian A (Hahn et al., 1986) to at least the Stephanian (Briggs and Almond, 1994; but also see Barthel and Schneider *in* Barthel and Rössler, 1995). Despite the widespread distribution of body fossils of *Arthropleura* in Europe, body fossils have previously been described from only two localities in North America: the Mazon Creek region, Illinois (Westphalian D; Desmoinesian in Midcontinent terminology), and Springhill, Nova Scotia (Westphalian B; Atokan in Midcontinent terminology).

Trackways produced by *Arthropleura* have been recorded from Fife, Scotland (Viséan; Pearson, 1992); Arran, Scotland (Namurian); Montceau-les-Mines, France (Stephanian B; Briggs and Almond, 1994); Joggins, Nova Scotia (Westphalian B; Ferguson, 1975); and Gardner Creek, New Brunswick (Westphalian A or B; Briggs et al., 1984). Based on the occurrence of body and trace fossils, the stratigraphic range of *Arthropleura* is Namurian A (Viséan) to at least the Stephanian (Ross and Briggs, 1993; Briggs and Almond, 1994). The paleoecology of *Arthropleura* has been discussed in a number of papers, including Rolfe (1985) and Shear and Kukalová-Peck (1990).

The purpose of this paper is to describe two specimens of *Arthropleura* from the Appalachian Basin of North America and to briefly review other North American reports of the genus.

In 1956, Richardson described specimens of *Arthropleura* from the Mazon Creek, Illinois, fauna. He subsequently (1959) named a new species, *A. cristata,* from the Mazon Creek area, designating a specimen consisting of a partial paratergal fold (FMNH PE 5262), as the holotype. Based on size and geographic association, Richardson also referred previously described arthropleurid material, consisting of a limb (now USNM 439582) and portions of plates (FMNH PE 9303 and 9304) that would have been associated with limbs in life, from the Mazon Creek area to that same species. While it is certainly likely that all these Mazon Creek specimens are conspecific, proof awaits a specimen that bears well-preserved, associated limb and tergal material. Nevertheless, Richardson's reasoning for referral of all of this material to the same species is plausible; therefore, I am following his conception of the species.

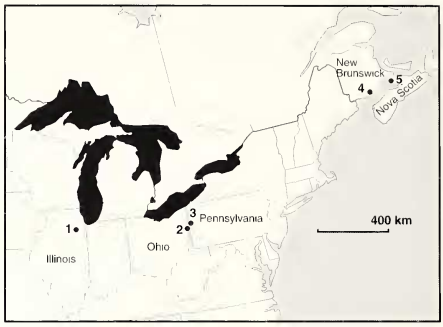

Figure 1. North American localities from which body fossils of *Arthropleura* and trace fossils thought to have been produced by *Arthropleura* are known. 1. Mazon Creek region, Illinois, body fossils described by Richardson (1956, 1959). 2. 7-11 Mine, northeastern Ohio, occurrence first noted by McComas and Mapes (1985), body fossil described in this paper. 3. Cannelton, Pennsylvania, body fossil described in this paper. 4. Gardner Creek, New Brunswick, *Diplichnites,* a trackway ascribed to *Arthropleura,* described by Briggs et al. (1984). 5. Springhill, Nova Scotia, body fossil described by Copeland (1957); and Joggins, Nova Scotia, trackways noted by Ferguson (1975).

In 1957, Copeland described and illustrated (p. 52; Pl. XV, fig. 2) a small (23 mm long) specimen of *Arthropleura* from Springhill, Nova Scotia. The specimen, consisting of portions of several tergites in dorsal view, was originally assigned to the genus *Amynilyspes* Scudder. Rolfe (1969, p. R617) subsequently corrected the generic identification, assigning it to the genus *Arthropleura.* Judged by Copeland's photograph and description of this specimen, its spinosity and tuberculation is somewhat similar to that of *A. cristata.* The incompleteness and large size of the holotype of *A. cristata,* however, hampers com-

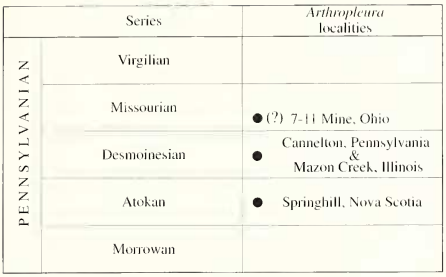

Figure 2. Chart showing stratigraphic distribution of body fossils of *Arthropleura* found in North America. Midcontinent (USA) terminology is used.

parison between the Mazon Creek and Nova Scotia forms.

Schultze (1972, p. 94) noted the occurrence of a fragmentary fossil tentatively identified as *Arthropleura* from the upper part of the Escuminac Formation (Upper Devonian) of the Escuminac area, Quebec. This fragment does not belong to an arthropleurid (Rolfe *in* Jeram, 1996, p. 110), but instead is a part of an unidentified chelicerate. *Eoarthropleura* is found, however, on the New Brunswick side of Escuminac Bay, in what may be Emsian strata (Shear and Selden, 1995, p. 373).

Arthropleura has previously been noted as occurring in Ohio at the 7-11 Mine (McComas and Mapes, 1988) and arthropleurid remains have been noted as possibly occurring at Linton, Ohio (Hook and Baird, 1988, p. 57). The 7-11 material is described here. The Linton occurrence, which has been cited subsequently in comprehensive lists of taxa found at Carboniferous sites, e.g., by Schultze and Maples (1992, appendix 1), is probably not valid. Donald Baird, who has studied Linton fossils over a 40-year period, has never seen an authentic specimen of *Arthropleura* from that site, and feels that the report of *Arthropleura* at Linton may have been based on a misidentification (D. Baird, personal communication, 1993). North American localities with verifiable occurrences of body or trace fossils which can be ascribed to *Arthropleura* are plotted on Figure 1. The stratigraphic distribution of body fossils of *Arthropleura* found in North America is shown in Figure 2.

Terminology used here follows that of Rolfe (1969, see especially fig. 390), which is based on that of previous workers, including Waterlot (1934). As used here, the terms plate and lobe, and the lettering of the lobes of the rosette plate, have no particular functional implication. Abbreviations used in this paper are: CaMNH Carnegie Museum of Natural History; FMNH, Field Museum of Natural History; YPM, Yale Peabody Museum; USNM, U.S. National Museum of Natural History.

Systematic Paleontology

Class ARTHROPLEURIDEA Waterlot, 1934 *(nom. correct.)*
Order ARTHROPLEURIDA Waterlot, 1934

Remarks

Rolfe (1969) revised the higher order classification of this group, placing Guthörl's (1934) order Gigantopleurida in synonymy with Waterlot's (1934) order Arthropleurida. However, Rolfe considered the Arthropleurida to be a class. Later, Stormer (1976, p. 90) placed the order Arthropleurida in the identically spelled class Arthropleurida. Subsequently Hahn et al. (1986) placed the order Arthropleurida in the identically spelled subclass Arthropleurida. More recently, Shear and Selden (1995) named a new order of arthropleurid, the Eoarthropleurida, and used the name Arthropleurida at class level. The name Arthropleurida is here used to designate the order, retaining Waterlot's (1934) designation at its original ordinal level. A slightly different term, Arthropleuridea, is used at the class level to avoid confusion (this emendation has been suggested by William Shear, personal communication, 1996).

Family ARTHROPLEURIDAE Zittel, 1885
Genus *ARTHROPLEURA* Jordan *in* Jordan & Meyer, 1854

Diagnosis

Small to large multisegmented arthropods with approximately 30 wide tergites. Numerous limbs, each consisting of 8-10 segments. Several plates, including multilobed rosette plates, located at base of legs.

Discussion

The nomenclatorial histories of the genus and the type species were reviewed by Hahn et al. (1986).

ARTHROPLEURA CRISTATA Richardson, 1959
Figures 3-5

Arthropleura sp. RICHARDSON, 1956, p. 72-76, fig. 39, 40; ROLFE & INGHAM, 1967, Pl. 1, fig. 7; ROLFE, 1969, figs. 391b-c.
Arthropleura cristata RICHARDSON, 1959, p. 79, figs. 42-43; LANGFORD, 1963, p. 19, figs. 22-24.

Material studied

CaMNH 33853, consisting of a rosette plate with attached B plate as well as a smaller (?)limb fragment, both closely associated on the same slab. Counterpart, consisting primarily of a mold of this material, present on matching slab. Collected by Gregory A. McComas from the 7-11 Mine, a strip mine in Columbiana County, Ohio (Carnegie Museum stratigraphic locality [SL] no. 2087). This locality is located 1.1 km north of the intersection of

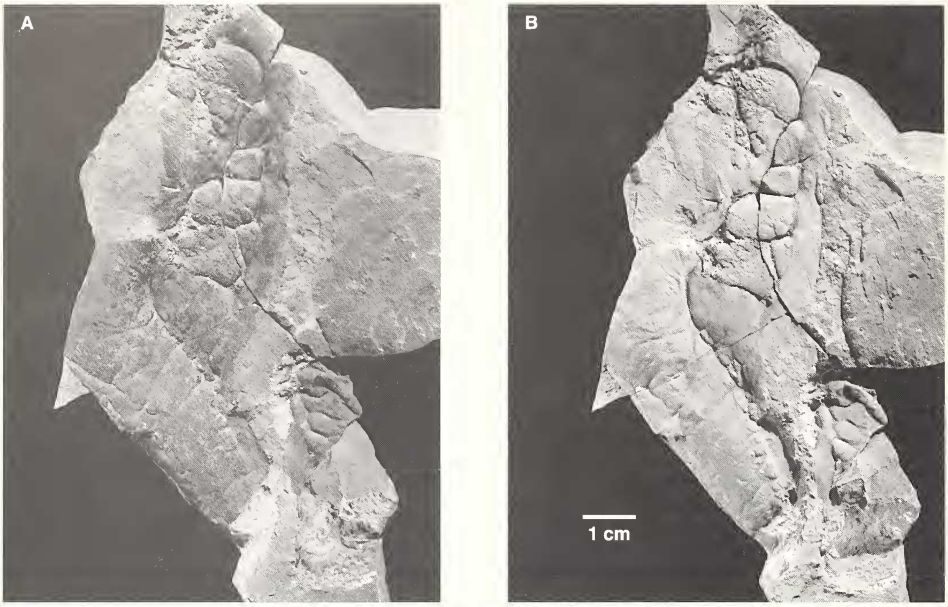

Figure 3. *Arthropleura cristata* Richardson, CaMNH 33853, collected at the 7-11 Mine, northeastern Ohio, by Mr. Gregory McComas. A, specimen unwhitened; B, specimen whitened. Specimen consists of a rosette plate with an attached B plate as well as a smaller (?)limb (appendage) fragment.

Ohio routes 7 and 11. The specimen, preserved in medium dark gray shale, was found as float, but G. McComas (personal communication) has been able to trace the lithology to a dark shale ("Brush Creek") in a high wall in the mine. The "Brush Creek" is lower Conemaugh (?Missourian).

Plant fragments, including *Lepidophyllum* sp. (S. Chitaley, Cleveland Museum of Natural History, personal communication, 1996), and small conchostracans are also found on the slab containing the arthropleurid. Walchian conifers, ostracods, insects, and other arthropods are found in the dark shale at this locality; additional information on the locality and its flora and fauna is given in McComas (1988) and McComas and Mapes (1988).

Description

Right B plate and attached rosette plate (Figures 3, 4) very large for genus. Length of entire preserved section 95 mm. B plate (left side of Figures 3A&B, 4) 72 mm long, subrectangular, with straight, rounded posterior edge; bulbous extension of B plate abuts posterior border of rosette plate; row of large but subtle tubercles arranged in linear fashion, beginning close to triple intersection of B plate with I lobe and anterior border of rosette plate, and extending toward proximal margin of B plate (Figures 3A&B, 4; left side of Figure 5), several wrinkles extend posteriad from between tubercles and from intersection of I lobe and B plate, otherwise smooth to very low tuberculation. Length of anterior border of rosette plate (=length of entire preserved section of rosette plate) 71.6 mm. Rosette plate (Figures 3, 4) with prominent, wide, anterior and posterior borders and five major lobes. Anterior border mostly smooth, posterior border with small tubercles. I lobe subtriangular, 18.7 mm long measured along long axis and about 15 mm wide at widest point, with corner abutting anterior border of B plate produced distally; several large tubercles located along border with B plate, remainder subtly wrinkled. C lobe irregularly five-sided, 14.4 mm long and 10.5 mm wide, covered with fine tubercles. Triangular lobe, 7.9 mm long and 4.1 mm wide, intercalated between C and E lobes along anterior border of rosette plate. E lobe subrectangular, 14.7 mm long and 8.6 mm wide, with three large low tubercles on or near anterior. E_2 lobe 14.4 mm long

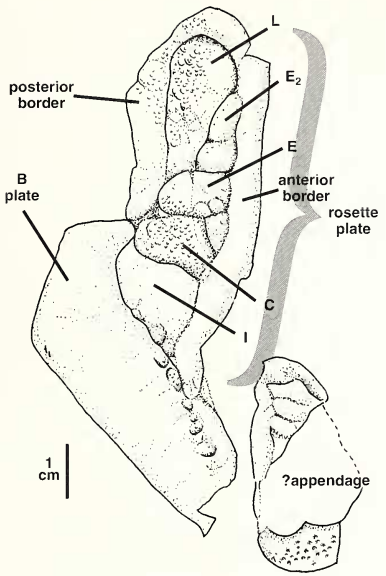

Figure 4. Sketch identifying parts of *Arthropleura cristata* Richardson, CaMNH 33853. Lettering of the rosette plate and other terminology follows that of Rolfe (1969).

and 6.8 mm wide at widest point, tuberculate, divided into two subequal parts by horizontal sulcus. L lobe irregularly and narrowly triangular, widening distally, 27.1 mm long and 13.3 mm wide; most of lobe covered by fine tubercles, proximal end also has several large low tubercles.

Another, partially preserved (?)limb (bottom right of Figures 3A&B, 4; right side of 5), elongate, with exterior surface of one end composed primarily of three parallel lobes flanked by rounded borders on two sides. Internal end of opposite side concave, with rounded, distal border and proximal border consisting of two lunate invaginations joining at midpoint, interior of this integument punctate. Exposed area of reverse side smooth. Triangular area, 24.8 mm long and 9.7 mm wide at base, preserved as mold on counterpart of fossil adjacent to lobate region (right side of Figure 5).

Discussion

The ventral side of the B plate is illustrated in Figures 3 and 4. The more-or-less straight, rounded posterior edge of the plate curves around the end of the fossil onto the other side of the rock slab where it terminates as a straight rim. The partially preserved (?)limb (bottom right of Figures 3A&B, 4; right side of Figure 5) with its adjacent triangular integument is difficult to interpret because of its fragmentary nature. Although it is preserved near the proximal side of the B plate, this (?)limb does not appear to be attached to the B plate. The concave, punctate region of the (?)limb may be an interior view of a part of a spinous or tuberculate leg segment. The triangular integument (right side of Figure 5) may represent an adjacent part of the ventral integument of the animal. The occurrence of the (?)limb near the proximal side of the B plate, and its enigmatic shape, argue against its being part of the same leg as the B plate and attached rosette organ.

Species of *Arthropleura* are distinguished primarily by the shape, spinosity, and tuberculation of the tergites (see, for instance, Waterlot, 1934, p. 105; and Richardson, 1959). Although both tergal and limb material have been recovered from the Mazon Creek deposits, the material is not articulated.

The rosette plate of this specimen is very close in size, overall configuration, and pattern of tuberculation to a very large left rosette plate in the collections of the Field Museum of Natural History, PE 9304 (Rolfe and Ingham, 1967, plate 1, fig. 7; Rolfe, 1969, fig. 391C) that Richardson referred to *Arthropleura cristata*. For instance, in both specimens the C lobe, the L lobe, and the part of the posterior border adjacent to the L lobe, are covered with fine tubercles. A similar pattern, likely based on Mazon Creek specimens, has been depicted by Rolfe (1969, fig. 390). There are differences between the two specimens, however, the most notable being the smaller E lobe of the Ohio specimen. Also, the L lobe of the Ohio specimen is larger and less deeply dissected than that of PE 9304. The differences between the Ohio specimen and PE 9304 are of lesser magnitude, however, than the differences between PE 9304 and smaller individuals from Mazon Creek, for instance PE 154 (Richardson, 1956, fig. 40a&b; Rolfe, 1969, fig. 391B) and PE 153 (Richardson, 1956, fig. 40c&d).

The tuberculation of the lobes of the rosette plate and of the B plate of this specimen, while very close to that of PE 153, is reduced compared to that of USNM 439582 (Richardson, 1956, fig. 39), which represents a smaller, but still large, *Arthropleura* from Mazon Creek. This is contrary to the general trend of increasing tuberculation with size observed by Rolfe (1969, p. R613), but this can be ascribed to intraspecific variation.

Thus, the Ohio specimen is well within the range of variation of material found at Mazon Creek. It is certainly conspecific with specimens consisting of rosette plates, including PE 9304, that Richardson (1959) referred to *A. cristata*. It is possible that the species *A. cristata* is con-

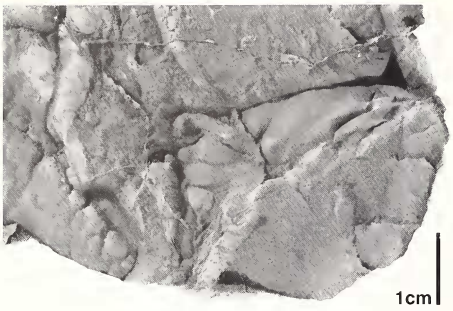

Figure 5. *Arthropleura cristata* Richardson, latex cast of part of CaMNH 33853. Whitened. Left side of photograph shows proximal part of B plate with row of large but subtle tubercles. Middle and right of photograph shows smaller (?)limb (appendage) fragment (also seen in bottom right hand corner of Figures 3A&B) and attached triangular portion of what was originally integument (not seen in Figure 3).

specific with *Arthroplenra springhillensis* (Copeland, 1957). The ornamentation on the dorsal surface of the tergites of the small species *A. springhillensis* (Copeland, 1957), which is based on several partial tergites, closely resembles that of *A. cristata.*

The pattern of tuberculation of the paratergal lobes of *A. cristata* from Mazon Creek is also similar in some ways, especially in the distribution of large and small tubercles, to that of *A. armata* Jordan. Also, the pattern of tuberculation of the paratergal lobes of *A. armata* has also recently been suggested to be variable and not as important as previously assumed for taxonomy (Hahn et al., 1986). This suggests that a reanalysis of described species of the genus is in order. The mode of preservation of the Ohio material, as a black film on a medium dark gray matrix along with carbonized plant material, is also similar to that of type material of *A. armata* housed in the collections of the Museum für Naturkunde, Berlin. This suggests similar habitats and modes of burial for the Ohio and German material.

Because a detailed analysis of Canadian and European material is beyond the scope of this paper, existing usage of the species *A. cristata* is retained here.

Size of the Arthropleura

Size of the arthropleurid from which this specimen is derived can be calculated by various means. Scaling problems are inherent with any such determination, however, and one must expect that there would be interspecific, intraspecific, and ontogenetic variations in proportions of limb sizes versus total body length. Also, the limbs of arthropleurids have been shown to vary greatly based on position (Briggs and Almond, 1994).

The length of the anterior border of the rosette plate of the Ohio specimen, measured from the intersection of its posterior margin with the B plate to the most distal point of the anterior border opposite that intersection point, is 65 mm. The length of the anterior border of a well-preserved Mazon Creek specimen (USNM 439582) is about 36 mm. The entire leg complex of the USNM specimen is about 127 mm. Assuming similar proportions, the Ohio leg would have been 229 mm long. Such a leg would belong to an animal whose tergites would be a minimum of 458 mm wide, that is, the length of two legs. Consideration of the sternal plates would add width, as the legs would be separated by sternites. However, if the legs projected from the tergites, as seen in some reconstructions (e.g., Rolfe, 1969, fig. 387; Hahn et al., 1986), the additional width added would be reduced. The legs do not project from beneath the tergites in the reconstruction of Almond and Briggs (1994, fig. 2). That reconstruction, however, is based upon juveniles which were much smaller than the specimens studied here. Using the proportions of the reconstruction of Rolfe and Ingham (1967; fig. 387 in Rolfe, 1969) the length of a specimen with a width of 458 mm would slightly exceed 1.5 m. The estimated length of the specimen would be longer (greater than 2 m) using the length-to-width ratio of the more elongate reconstruction of Hahn et al. (1986, Abb. 2). Also, the number of segment numbers borne by adults of the genus are not known with certainty. Hahn et al. (1986) estimated a minimum number of 30 body somites for *Arthroplenra armata* Jordan, but this and other species may have had additional segments. Thus, the true length of the specimen described here may have been even longer.

ARTHROPLEURA cf. *A. CRISTATA*

Figure 6

Material studied

YPM-PU 88076, formerly at Princeton University, now in the Yale Peabody Museum's Entomology collection. The specimen consists of a partial left rosette plate, an attached partial B plate, a disarticulated K plate, and an elongate, disarticulated fragment that may or may not belong to the specimen. The specimen was preserved on two counterparts, one of which (marked with an old no., M. 855) was examined as part of this study. A latex mold of the Yale specimen made by Donald Baird, FMNH PE 26148 (Figure 6), was also examined as part of this study. According to the Yale and Field Museum labels, the specimen was collected by I. F. Mansfield in 1877 from his mine at Cannelton, Darlington Township, Beaver County, western Pennsylvania. The specimen is preserved in a

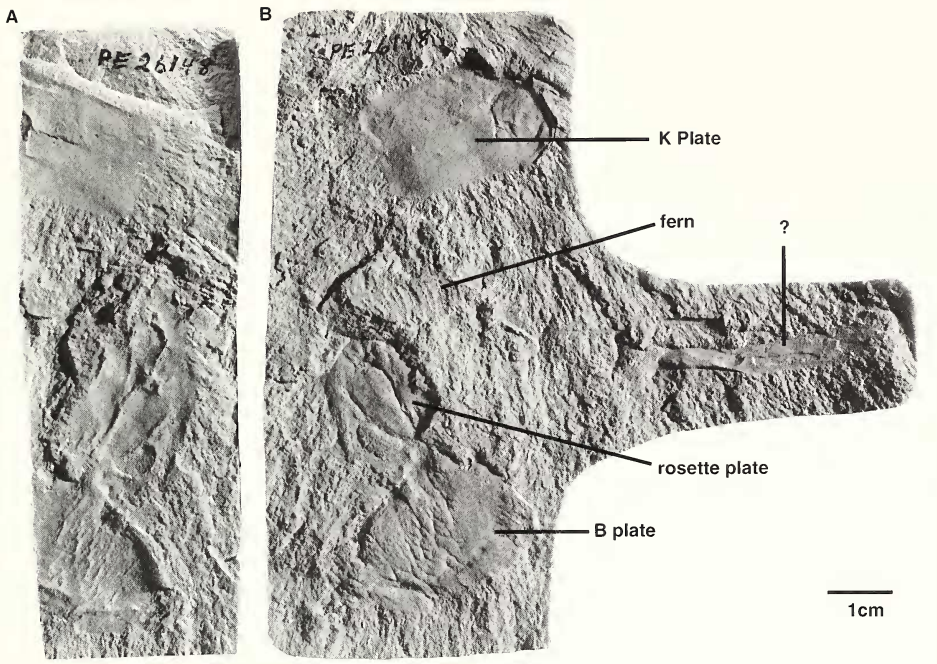

Figure 6. *Arthropleura* cf. *A. cristata*. FMNH PE 26148 (a latex cast of YPM-PU 88076), from Cannelton, western Pennsylvania. Collected by I. F. Mansfield. Molds of part (A) and counterpart (B). Specimen includes a partial rosette plate, an attached partial B plate, a disarticulated K plate, and an elongate, disarticulated fragment (indicated by a "?") that may or may not be related to the specimen. A fern is also present.

grayish black shale ("cannel slate") found below an Upper Kittanning cannel coal within the Kittanning Formation, Allegheny Group, Middle Pennsylvanian (approximately middle Westphalian D, Baird, 1978, p. 14; or Desmoinesian in Midcontinent terms).

Fragments of plant material, including a fern fossil, are preserved on the slab containing the arthropleurid. The fern is located between the K plate and the rosette plate/B plate, just below the level of the arthropleurid material. The Cannelton locality has yielded a number of plants, eurypterids, insects, and fish. Additional information on this locality and its fauna can be found in Baird (1978).

Description

Left B plate and closely associated rosette plate (bottom of Figures 6A&B), and separated K plate (top of Figures 6A&B), large for genus. B plate subrectangular, preserved section about 30 mm long and 23 mm wide, midsection coarsely covered with large but subtle tubercles; thin groove, approximately 4 mm from edge, runs along posterior. Rosette plate with prominent anterior border and several preserved lobes. (?)C lobe subovate, 7.7 mm long (maximum length) and 3.9 mm wide, covered with fine tubercles. (?)E lobe subtriangular, 14 mm long and 7 mm wide (maximum width), with acutely pointed posterior corner. Small, 2.9 mm x 8 mm, triangular lobe intercalated between presumed C and E lobes and anterior border. Other lobe(s) of rosette plate indistinct. K plate subrectangular, mostly smooth, with rounded rims; rims on the (?)distal side more strongly rounded. Maximum width 30 mm, 17.6 mm long at midpoint. Proximal edge straight; distal edge curved. Two subcentrally located par-

allel longitudinal ridges join Y-shaped ridge near distal side (Figures 6A&B).

Discussion

The rosette and B plates of this specimen are incomplete, making interpretations of specific features difficult. It is difficult to be sure that the lobe identifications are correct. The ridges on the K plate may be taphonomic.

An elongate object (labeled "?" on Figure 6), 37 mm long and 5.4 mm wide, with longitudinal wrinkling, is associated with the specimen. Its mode of preservation as a black film is similar to that of the certain arthropleurid material. It is possible that this elongate object may represent a part of the arthropleurid, for instance the edge of a tergite.

The Pennsylvania specimen is smaller than the Ohio specimen. Except for the greater rugosity of its B plate, the Pennsylvania specimen is of about the same overall rugosity. That greater rugosity of the B plate, however, is less than that of the B plate of USNM 439582, a specimen from Mazon Creek. The Pennsylvania material is flattened more than the Ohio material and is preserved in a darker shale. But, like the Ohio material, it is preserved as a thin black film. The Pennsylvania specimen may be conspecific with the Ohio and Illinois material, but final determination awaits additional material.

Based on USNM 439582, the length of the K plate of *Arthropleura cristata* is subequal to the length of the rosette plate. If the Pennsylvania specimen is conspecific, the reconstructed length of that specimen would then be about half the size of the specimen from Ohio; that is, the minimum length of the reconstructed animal would be a little less than 0.75 m. Proportions based on the C lobe of the Ohio specimen and the questionable C lobe of the Pennsylvania specimen would give a roughly similar figure, giving credence to this minimum length. Using measurements of the K plate of other species of *Arthropleura* give different figures. The K plate of a specimen of *Arthropleura uanmata* (Salter) from the Netherlands that was described and illustrated by Hahn et al. (1986, Abb. 3) has reconstructed dimensions of 60 by 40 mm, representing, according to Hahn et al., an animal with a total length of >2 m. The K plate of the Pennsylvania specimen has dimensions roughly ½ of those of that specimen from the Netherlands. Using these proportions the minimum length of the Pennsylvania specimen would be somewhat longer than 1 m.

Conclusions

The specimens described here extend the geographic and stratigraphic range of *Arthropleura* in North America. The geographic range of the species *A. cristata* is extensive; the Mazon Creek site is 650 km from the 7-11 site. The stratigraphic range of body fossils of *Arthropleura* found in North America extends from the Atokan into what is probably the lower Missourian. This stratigraphic range is well within that reported for European occurrences of body fossils of *Arthropleura*.

Acknowledgements

Work on this paper would not have been possible without the kindness extended by Mr. Gregory A. McComas of Marion, Ohio, who not only discovered the Ohio specimen and donated it to the Carnegie Museum of Natural History, but also provided information on the 7-11 site and its stratigraphy. Donald Baird, Pittsburgh, Pennsylvania, called attention to the specimen from Pennsylvania, which had been originally identified as *Arthropleura* by W. D. Ian Rolfe. Dr. Baird also provided information on the Pennsylvania locality and the Linton site. Jann Thompson, U.S. National Museum of Natural History; Gregory Buckley, Field Museum of Natural History; John Carter and Albert Kolar, Carnegie Museum of Natural History; and Erika Pietrzeniuk, Museum für Naturkunde, loaned specimens and/or facilitated visits to their respective institutions. Russell White, Yale Peabody Museum (YPM), located the original specimen from Pennsylvania, which was loaned by Raymond Pupedis (YPM). Photographs were taken by Bruce Frumker, The Cleveland Museum of Natural History (CMNH). David Condon and Suellen Hopfer (CMNH) provided translations, and Shya Chitaley (CMNH) identified plant material. This paper was improved by critiques or reviews by Derek Briggs, University of Bristol; William Shear, Hampton-Sydney College; Paul Selden, University of Manchester; R. M. Feldmann, Kent State University; and W. D. I. Rolfe, Edinburgh.

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